

Passive Flow Through an Unstalked Intertidal Ascidian: Orientation and Morphology Enhance Suspension Feeding in *Pyura stolonifera*

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Abstract. Passive flow is believed to increase the gains and reduce the costs of active suspension feeding. We used a mixture of field and laboratory experiments to evaluate whether the unstalked intertidal ascidian *Pyura stolonifera* exploits passive flow. We predicted that its orientation to prevailing currents and the arrangement of its siphons would induce passive flow due to dynamic pressure at the inhalant siphon, as well as by the Bernoulli effect or viscous entrainment associated with different fluid velocities at each siphon, or by both mechanisms. The orientation of *P. stolonifera* at several locations along the Sydney-Illawarra coast (Australia) covering a wide range of wave exposures was nonrandom and revealed that the ascidians were consistently oriented with their inhalant siphons directed into the waves or backwash. Flume experiments using wax models demonstrated that the arrangement of the siphons could induce passive flow and that passive flow was greatest when the inhalant siphon was oriented into the flow. Field experiments using transplanted animals confirmed that such an orientation resulted in ascidians gaining food at greater rates, as measured by fecal production, than when oriented perpendicular to the wave direction. We conclude that *P. stolonifera* enhances suspension feeding by inducing passive flow and is, therefore, a facultatively active suspension feeder. Furthermore, we argue that it is likely that many other active suspension feeders utilize passive flow and, therefore, measurements of their clearance rates should be made under appropriate conditions of flow to gain ecologically relevant results.

Introduction

The gain and use of energy influence the fitness of all organisms (Townsend and Calow, 1981; Sibly and Calow, 1986). The net gain from feeding depends on how much food an animal consumes and assimilates minus the costs associated with the capture, digestion, and absorption of food, as well as the discarding of waste (Sibly, 1981; Townsend and Hughes, 1981; Sibly and Calow, 1986). For active suspension feeding invertebrates, there is the potential, by using external water movement, to increase the food consumed or reduce the costs of feeding, or both (Vogel and Bretz, 1972; Allanson *et al.*, 1992; Vogel, 1994). Active suspension feeders must pump water across their filtering structures to feed, which incurs a metabolic cost (Jørgensen, 1966; Wildish and Kristmanson, 1997). Passive flow induced by external water movement (Vogel, 1974) may, however, enable active suspension feeders to augment the flow of water through their filtering structures, hence increasing their feeding rate or reducing the energy required to move water actively, or both (Vogel and Bretz, 1972; Vogel, 1974, 1994; LaBarbera, 1977, 1984; Wildish and Kristmanson, 1997).

Active suspension feeders, such as solitary ascidians, could induce passive flow from external water movement in several ways (Vogel and Bretz, 1972; Vogel, 1974, 1994). The most obvious is by orienting the inhalant siphon into the flow and the exhalant siphon away from the flow. The resultant dynamic pressure on the inhalant siphon would force water through the ascidian (Vogel, 1974, 1994; Kott, 1989). The stalked ascidian *Styela montereyensis* has been shown to use dynamic pressure (Young and Braithwaite, 1980). The stalk of *S. montereyensis* enables it to orient its inhalant siphon into the prevailing current by the force of water movement alone. Ascidians without stalks have fixed

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orientations and, as a result, induction of passive flow may be more constrained. Yet many marine habitats, both intertidal and subtidal, experience water movement that can be predictable in both direction and strength (Wainwright and Dillion, 1969; Denny, 1988). In such habitats, there is the potential for unstalked ascidians to use dynamic pressure for assisted feeding, but this has not yet been demonstrated. The Bernoulli effect and viscous entrainment (Day, 1974; Vogel, 1978, 1994; Kott, 1989) may also enable unstalked ascidians to induce passive flow from external water movement by positioning their exhalant siphons higher above the substratum than their inhalant siphons (Vogel, 1974, 1977; Allanson *et al.*, 1992).

Pyura stolonifera (Heller, 1978) is the common solitary ascidian found on intertidal rocky shores along the east coast of Australia (Kott, 1985). This unstalked ascidian has its inhalant siphon directed horizontally and its exhalant siphon higher and directed vertically (Fig. 1; Day, 1974; Kott, 1985). Furthermore, casual observations suggested that the inhalant siphons of these ascidians were usually directed into the oncoming waves. We predicted that this arrangement and orientation of the siphons would induce passive flow through the ascidian. To evaluate whether *P.*

stolonifera induces passive flow from the movement of water over intertidal shores, we investigated four questions: (1) whether the ascidian was nonrandomly oriented, (2) whether the arrangement of the ascidian's siphons was capable of inducing passive flow, (3) whether the orientation of the ascidian affects the magnitude of passive flow, and (4) whether its orientation into the flow increases its feeding rate on the rocky shore.

Materials and Methods

Field orientation

We surveyed the orientation of *Pyura stolonifera* at six rocky shores covering a wide range of wave exposures and orientations along the Sydney-Illawarra coast (Fig. 2). The orientation of the ascidian, defined as the direction of the axis running from the exhalant to the inhalant siphon, was measured to the nearest 5° using a magnetic compass. At each shore, the *P. stolonifera* population was sampled representatively using at least five 1-m² quadrats positioned randomly along a 50-m transect laid out parallel to the shoreline within the population. In each quadrat, the orientation of all ascidians and the direction of the waves coming

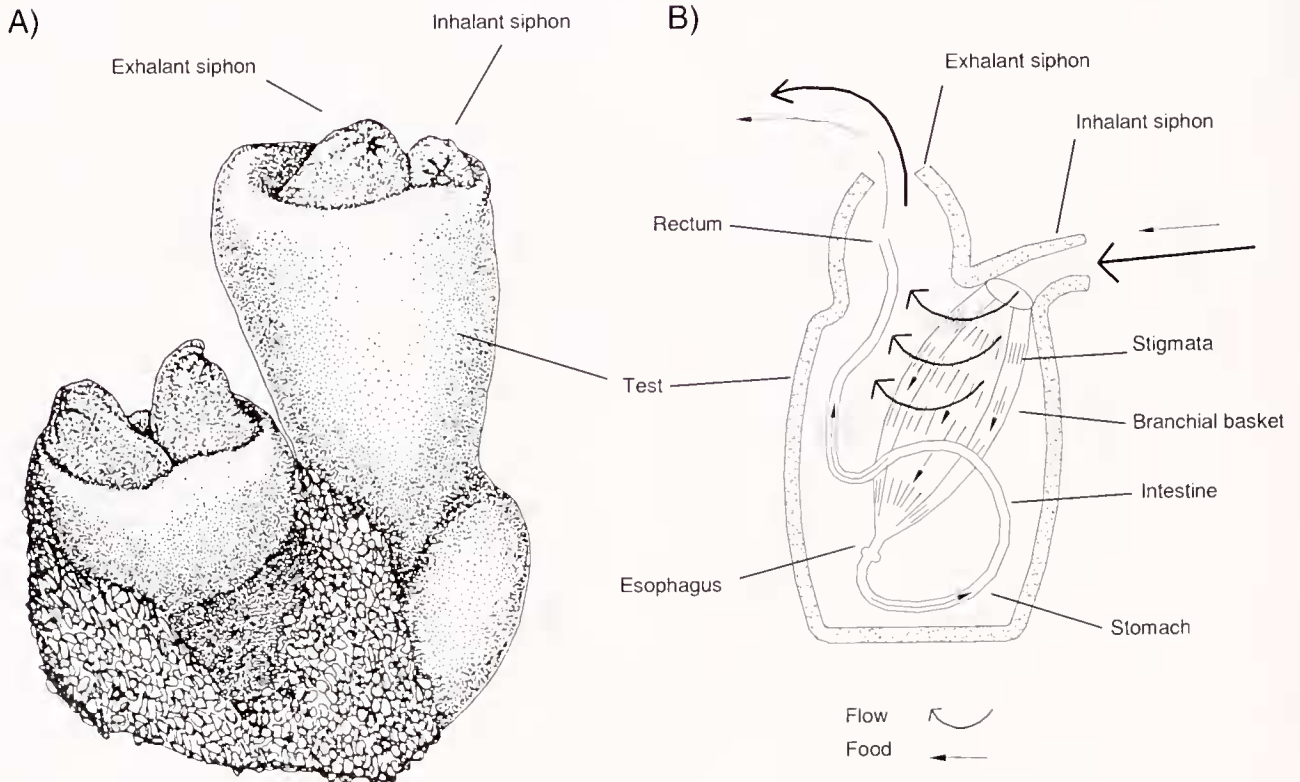


Figure 1. Morphology of the intertidal ascidian *Pyura stolonifera*. (A) Diagram of the external morphology of non-feeding animals with partially retracted siphons (reprinted with permission from P. Kott and Museum of Queensland Press; Kott, 1985). (B) Schematic diagram showing the internal structure of the ascidian and the pathways for water and food through the ascidian. The exhalant siphon is projected directly upwards, and the inhalant siphon is projected parallel to the substratum.

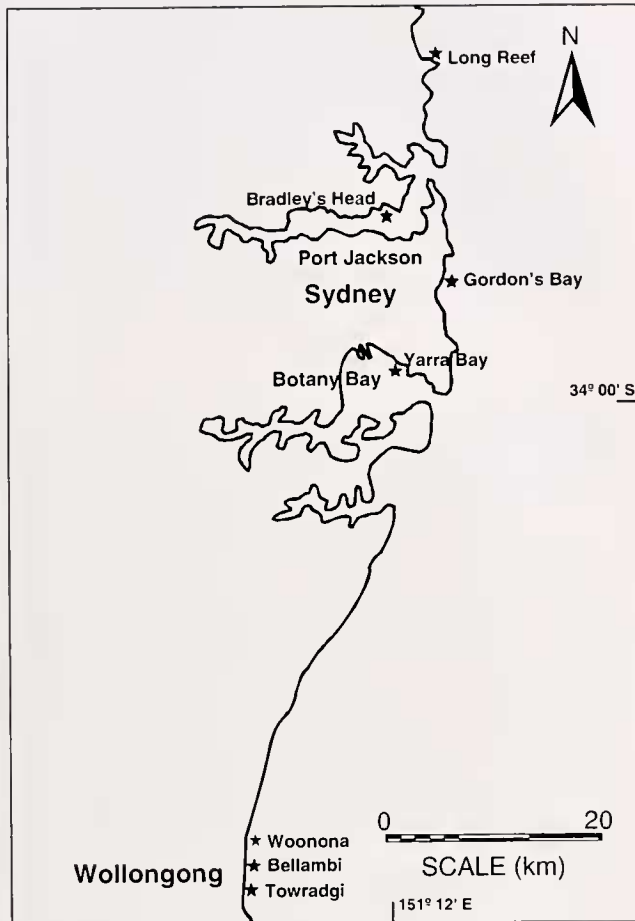


Figure 2. Study locations along the Sydney-Tllawarra coast.

onto the shore at the time of sampling were measured. Because the direction of the waves varied along the transect, the measurements of the ascidians in each quadrat were standardized against the mean wave direction of the quadrats across the whole transect. The orientations of more than 240 individuals of *P. stolonifera* were measured at each shore.

Flume experiment

To evaluate whether the morphology of *P. stolonifera* could induce passive flow, we used a flume and functional wax models of the ascidian. This enabled us to simplify the investigation of the ascidian's potential to induce passive flow. Also, we used models instead of real animals because the models could not play any active role in producing flow.

Models were cast from five live ascidians that were selected haphazardly from populations at Bellambi and Woonona (Fig. 2) and covered a representative range of sizes (test height 3–10 cm; test diameter 4–7 cm). Models were hollow, microcrystalline wax castings from alginate molds of the ascidians. Inside each model, tubing (5-mm

diameter) connected the inhalant opening to a reservoir (a 50-ml plastic bottle) and the reservoir to the exhalant siphon.

The reservoir was filled with blue food dye; we reasoned that, when the model was placed in the flume, any water movement through it would dilute the dye. The relationship between the dilution of the dye and the amount of water that moved through each model was calculated by passing set amounts of water (5–80 ml) through each model and spectrophotometrically measuring the absorbance of the reservoir contents after each run. This relationship proved to be very strong, with the coefficient of determination (r^2) for each model being greater than 0.995.

To evaluate whether the arrangement of the siphons of *P. stolonifera* was capable of exploiting passive flow, we tested the hypothesis that if the models were positioned within the directional flow of the flume, dye would escape from the exhalant siphon but not from the inhalant siphon. We also investigated whether the orientation of the ascidian influenced the magnitude of passive flow. We predicted that passive flow through the models would be greater when they were oriented with inhalant siphons into the flow (360°) than when oriented perpendicular to (90°) or away from (180°) the flow. The flow rate through each model was measured three separate times ($n = 3$) at each of these orientations. Replicate measurements were interspersed in terms of both models and orientations. Models were positioned in the flume for 5 min for each measurement.

The flow through the flume was laminar and reached free-stream velocity within 2 cm of the bottom and sides of the flume. The working section of the flume was 0.4 m deep, 0.3 m wide, and 3.5 m long, and along with the size of the models, satisfied the size requirements for flumes and experimental subjects set out by Nowell and Jumars (1987). The experiment was done at a mean flow speed of 15.2 cm s^{-1} with a standard deviation of 0.25 cm s^{-1} .

Field feeding experiment

We predicted that if passive flow enhances the feeding success of *P. stolonifera*, individuals oriented with their inhalant siphons into the waves would consume more food than those oriented perpendicular to the waves. To test this hypothesis, we positioned ascidians on the intertidal shore at Bellambi so that they were oriented into (360°) or perpendicular to (90°) the wave direction and measured their subsequent fecal production to infer their feeding rate (as described in Young and Braithwaite, 1980).

Ascidians used in this experiment were collected from the rocky shore at Bellambi (Fig. 2). Each animal had its exterior cleaned carefully and was then held in a laboratory seawater system for 72 h. Within this period, the ascidians evacuate more than 90% of their gut contents ($n = 5$; N. Knott, unpubl. data). Ascidians were attached to heavy steel

plates (3 × 25 × 50 cm) with epoxy resin (Epirez). Four ascidians were attached to each plate: two oriented into (360°) and two perpendicular to (90°) the wave direction. The epoxy was allowed to set for 12 h and, at the next low tide, the ascidians were returned to the rocky shore at Bellambi. After 24 h, the ascidians were brought back to the laboratory and removed from the plates. Their exteriors were washed and they were submerged in separate beakers containing filtered seawater. After 72 h, the ascidians were removed from the labeled beakers, and the water and feces from each beaker were filtered. The filter paper was dried at 70 °C for 1 h and weighed to calculate the dry mass of the feces to the nearest milligram. The ascidians themselves were removed from their tests and dried at 70 °C for 5 d to obtain their dry body mass to the nearest milligram. There was no relationship between the dry mass of the ascidians and their fecal production for either treatment, so fecal production was used as a measure of feeding rate independent of dry weight.

To evaluate whether any effects of orientation on the feeding rate of *P. stolonifera* were temporally consistent, the experiment was repeated. Both experiments initially had 12 replicate ascidians with each orientation (360° or 90°). In the first experiment, the mortality rate was high (42%), probably because the epoxy resin was set with the steel bases submerged in the laboratory seawater system. Rust particles from the steel plates made the water cloudy and possibly affected the ascidians. In the second experiment, the epoxy was set in open air for 12 h and few ascidians died (8% mortality rate).

Data analysis

The orientation of *P. stolonifera* populations was tested using Rayleigh's Z-test for nonrandomness (Batschelet,

1981; Zar, 1984). Data from the flume and feeding experiments were analyzed using analysis of variance. The experimental designs are provided in the table captions for each analysis of variance. In the feeding experiment, blocks were not included as a factor because of the loss of replicate ascidians, primarily in the first experiment. The normality and heterogeneity of variances were assessed for both the model and the feeding experiments by using box plots and plots of the residuals against means (Quinn and Keough, 2002).

Results

Field orientation

Across a range of wave-exposed rocky shores, the orientation of *Pyura stolonifera* was consistently nonrandom (Table 1). Furthermore, the mean orientation of the ascidian was closely associated with the estimated wave direction at each location (Table 1). That is, *P. stolonifera* tended to be oriented with its inhalant siphons directed into or away from the wave direction. This is illustrated by the circular frequency graphs of the orientation of *P. stolonifera* at two rocky shores (Fig. 3). At some locations, the ascidians had a unidirectional orientation, tending mainly to be oriented into the wave direction (e.g., Long Reef, Fig. 3 and Table 1); at other locations, they had a bidirectional orientation, tending to be positioned into or away from the wave direction (e.g., Towradgi, Fig. 3 and Table 1). The variability in the orientation of the ascidians differed substantially among locations (*r* values, Table 1): for example, variation was low at Long Reef, but high at Bellambi.

Flume experiment

The arrangement of the siphons of *P. stolonifera* induced passive flow. Dye streamed out of the exhalant siphon of

Table 1

Orientation of *Pyura stolonifera* at six rocky intertidal shores of varying wave exposure along the Sydney-Illawarra coast

Location	Wave exposure	Orientation		Wave direction ^c	<i>r</i> ^d	<i>P</i> ^e	Sample size
		Mean value ^a	Type ^b				
Long Reef	High	12 ± 7°	Uni	30°	0.670	<0.001	264
Towradgi	High	162 ± 18°	Bi	150°	0.283	<0.001	387
Bellambi	Moderate	36 ± 26°	Bi	20°	0.233	<0.001	247
Gordon's Bay	Moderate	183 ± 11°	Uni	170°	0.506	<0.001	410
Yarra Bay	Low	311 ± 8°	Uni	300°	0.611	<0.001	411
Bradley's Hd	Low	112 ± 19°	Uni	90°	0.289	<0.001	261

^a Mean orientation of the populations ± the 95% confidence intervals. Calculated as per Zar (1984).

^b Uni = unidirectional orientation; Bi = bidirectional orientation.

^c Mean estimated wave direction along the sampled shoreline on the day of sampling.

^d *r* is a measure of the variance of the orientation of the population (a value of 1 means that all individuals have the same orientation as the mean, whereas a value of 0 indicates that the population is uniformly distributed).

^e *P* values from Rayleigh's Z test for random circular distribution (Zar, 1984).

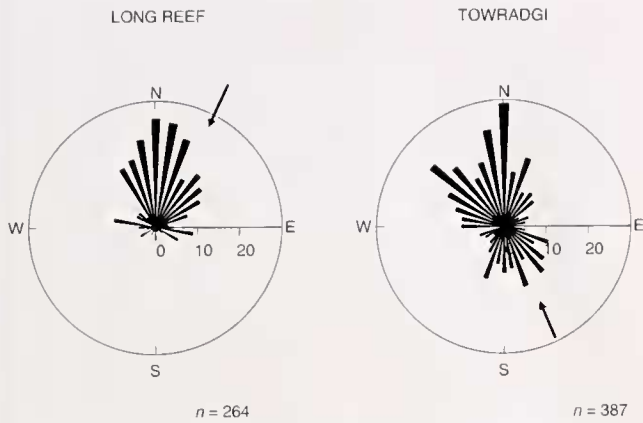


Figure 3. Circular frequency histograms of the orientation of *Pyura stolonifera* on two rocky intertidal shores. Arrows indicate the estimated wave direction at each shore on the day of sampling.

each model ascidian at all orientations (Fig. 4). Passive flow was, however, significantly greater through each model when oriented into the flow (360°) than when oriented perpendicular to the flow (90°) (Fig. 4; Table 2). Depending on the model, the difference in passive flow at these two orientations was 5- to 25-fold (Fig. 4). Some of the models showed relatively high rates of passive flow while oriented away from the flow (180°), but only one model, had significantly higher passive flow rates at this orientation than when oriented perpendicular to the flow (Table 2).

Field feeding experiment

Individuals of *P. stolonifera* oriented into the waves produced about twice as much fecal material as those oriented perpendicular to the waves, after being on the rocky shore for 24 h (Fig. 5; Table 3). This orientation effect was

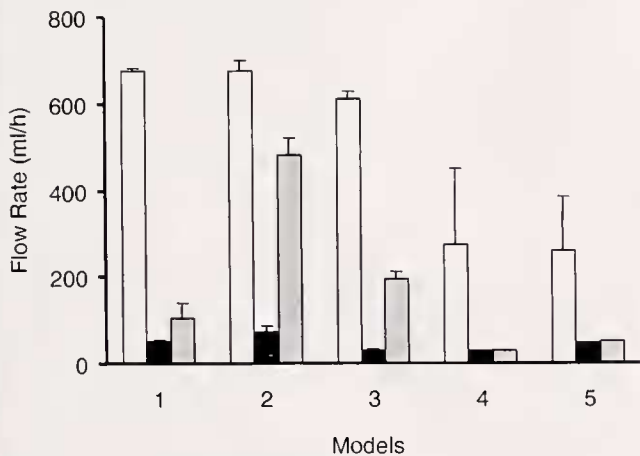


Figure 4. Passive flow (mean \pm s.e.; $n = 3$) through model *Pyura stolonifera* at three orientations in relation to flow through the flume. \square 360° , \blacksquare 90° , and \square 180° .

Table 2

Analysis of variance of passive flow through model Pyura stolonifera at three orientations in relation to the flow through the flume

Source	SS	DF	MS	F	P
Model	14.83	4	3.71	17.3	0.0000
Orientation	37.85	2	18.93	21.7	0.0006
Model \times Orientation	6.98	8	0.87	4.07	0.0022
Residual	6.42	30	0.21		
Pair-wise comparisons					
Model 1: $360 > 180 = 90$				Model 4: $360 > 180 = 90$	
Model 2: $360 > 180 = 90$				Model 5: $360 > 180 = 90$	
Model 3: $360 > 180 > 90$					

Orientation was a fixed factor with three levels (360° , 90° and 180°), and Model was a random orthogonal factor with five levels ($n = 3$). The data were transformed to $\log_e x$ to normalize the data and reduce the differences among variances. SNK tests were used to detect differences between means.

consistent even though the ascidians consumed less food in the first experiment than in the second (Fig. 5; Table 3).

Discussion

The unstaked ascidian *Pyura stolonifera* is a facultatively active suspension feeder (*sensu* LaBarbera, 1984) as it can actively pump water through its branchial basket by using its cilia, but its orientation and siphonal arrangement also induce passive flow. This conclusion is based on our results from laboratory and field experiments. First, on all rocky shores sampled, covering a large section of the Sydney-Illawarra coast (about 70 km) and a wide range of wave exposures, individuals of *P. stolonifera* were usually oriented into the waves. Second, our flume experiments demonstrated clearly that this orientation would maximize the

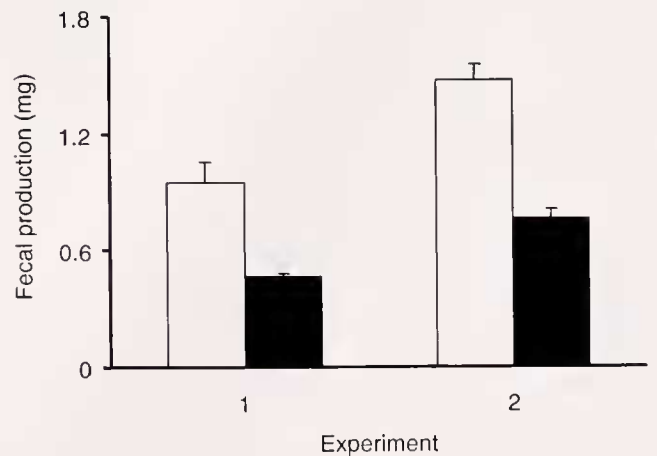


Figure 5. Fecal production (mean \pm s.e.) of *Pyura stolonifera* after 24 h at two orientations in relation to wave direction. Experiment 1, $n = 7$; Experiment 2, $n = 10$. \square 360° and \blacksquare 90° .

Table 3

Analysis of variance of the fecal production of *Pyura stolonifera* over 24 hours at two orientations on a rocky intertidal shore

Source	SS	DF	MS	F	P
Experiment	2.363	1	2.363	10.242	0.003
Orientation	2.901	1	2.901	13.386 ^a	0.001
Exp × Or	0.000	1	0.000 ^a	0.000	1.000
Residual	6.923	30	0.231 ^a		

Experiment (Exp) was a random factor with two levels, and Orientation (Or) was a fixed orthogonal factor with two levels—360°, 90°; $n = 7$ in Experiment 1, and $n = 10$ in Experiment 2. The data were transformed to $\log_e x$ to normalize the data and reduce the differences among variances.

^a The MS for the interaction between experiment and orientation appeared to be an underestimate ($P > 0.25$); therefore, this term was pooled with the residual to provide a more appropriate test for orientation (Un-derwood, 1997).

dynamic pressure on their inhalant siphons, producing the greatest passive flow through them. Finally, our field experiments confirmed that ascidians oriented into the wave direction had consistently greater feeding rates than those oriented perpendicular to the waves. Taken together, these findings suggest that passive flow is an integral aspect of the feeding strategy of this species. Our study is the first to demonstrate that unstaked ascidians utilize passive flow.

Although most of the *P. stolonifera* were oriented with their inhalant siphons directed into the waves, at some shores the ascidians were also oriented away from the waves. Wave action is the major determinant of flow in this environment; however, at some locations, the flow of water back down the shore after each wave is also substantial. We speculate that this backwash accounts for the bidirectional pattern of orientation observed at some locations (*i.e.*, Towradgi and Bellambi). This ascidian tends to form dense aggregations along rocky shores (Day, 1974; Kott, 1985) and individuals at the back of aggregations (away from the sea) were typically oriented into the backwash, while those at the front of the aggregation were usually oriented into the waves. Among individual ascidians, there was also variation in orientation that may be accounted for by small-scale local variation in flow across rocky shores. That is, the wave direction that individual ascidians experience may differ greatly over short distances due to the structure of the shore or aggregations of the ascidians themselves. The extent of intrapopulation variation in orientation (r , Table 1) differed substantially among locations, probably due to underlying differences in the consistency of the flow direction. This was most evident at Bradley's Head, where the orientation of the ascidians varied substantially, with most being oriented between 20° and 160°. This variation seemed to be reflected by the variation in the direction of the wave action due to the swash generated by passing ferries. During several hours of sampling, the direction changed frequently, by

about 90°. The apparent correlation between the orientation of the ascidians and the ferry swash suggests that human activities may have altered the orientation of the ascidians at this location. On the other shores, variation in wave direction could be generated naturally, although less frequently, by changes in wind and swell direction.

We predicted that *P. stolonifera* would be able to exploit passive flow not only due to dynamic pressure, but also because of the Bernoulli effect or viscous entrainment. Passive flow-through models did occur when they were oriented perpendicular to or away from the flow. This indicates that the Bernoulli effect or viscous entrainment, or both, can induce passive flow through the ascidian. Nevertheless, the magnitude of the passive flow at these orientations was much smaller for most models than when they were oriented into the flow.

We contend that the results from the models in the flume are a good indicator that the morphology of this ascidian enables it to exploit the movement of water over the rocky shore to induce passive flow. There were, however, several differences between the models and real individuals of *P. stolonifera* and between water movement through the flume and over rocky intertidal shores. For instance, the openings of the siphon in the models were smaller than those of real ascidians (up to 12 mm in diameter in live ascidians; N. Knott, pers. obs.); the exhalant siphons were shorter due to the models being cast from ascidians with partially retracted siphons (a normal reaction to being disturbed); and the models did not have branchial baskets. In relation to water movement, the flow through the flume was laminar with a relatively constant speed of 15 cm s⁻¹, whereas the flow conditions that the ascidians are exposed to on the rocky shore are often likely to be turbulent with flow speed exceeding 15 cm s⁻¹ (Denny, 1988). Given these differences, we needed to evaluate whether *P. stolonifera* was actually exploiting passive flow on rocky intertidal shores.

Our field experiments demonstrated enhanced feeding rates for individuals of *P. stolonifera* oriented into the waves on a rocky shore. This pattern was consistent across experiments despite the difference in the feeding rate between experiments, indicating that the ascidian's utilization of passive flow was temporally consistent. We believe, therefore, that it represents a general phenomenon for this ascidian.

The value of passive flow can be further demonstrated by comparing the active pumping rate of *P. stolonifera* specimens from a study in South Africa (Klumpp, 1984) and the passive flow rates measured through the model ascidians in our study. From Klumpp's data, the mean pumping rate of individuals with a dry weight of 3.8 g (the average dry weight of the ascidians used to cast the models in the current study) would be 1245 ml h⁻¹. Passive flow through the models was on average 498 ml h⁻¹ when orientated into the flow. Hence, it would appear that if the passive flow through

the models was representative of the passive flow through real ascidians, it could provide about 40% of the active pumping rate at a flow speed of 15.2 cm s^{-1} . Furthermore, passive flow through other facultatively active suspension feeders increases proportionally with external flow velocities (Vogel, 1974, 1977; Young and Braithwaite, 1980). Considering that the flow speed of water over the rocky intertidal is often much greater than that used in our flume experiment and that the actual siphon diameters are greater than those of the tubing we used, passive flow is likely to produce even more than 40% of the pumping rate in live animals.

The potential contribution of passive flow to suspension feeding is rarely considered in studies on invertebrate filtration or clearance rates (Klump, 1984; Famme *et al.*, 1986; Riisgard *et al.*, 1993; but see Reising, 1971, 1974). These rates are usually measured in still or very slow-moving water. Measurements made under such conditions may be appropriate for suspension feeding invertebrates that inhabit environments with little water motion (Famme *et al.*, 1986; Petersen and Riisgard, 1992); but many suspension feeding invertebrates inhabit environments that are almost continually exposed to fluid movement (Reidle, 1971; Vogel and Bretz, 1972; Vogel, 1976; Wildish and Kristman, 1997), which is often consistent in strength and direction (Wainwright and Dillion, 1969; Denny, 1988). Measuring the filtration and clearance rates of these suspension feeders in water with no or little flow will underestimate their real values if they utilize passive flow.

Early estimates of the metabolic costs of suspension feeding suggested that the costs may be only slightly less than the gains in energy (Jørgensen, 1966). Passive flow was, therefore, thought to benefit suspension feeders by reducing the energetic cost of pumping water (Vogel, 1974, 1977; Young and Braithwaite, 1980). Recent estimates of energy expended for suspension feeding have, however, put the costs at less than half a percentage point of the metabolic rate of most suspension feeders (Riisgard *et al.*, 1993; Riisgard and Larsen, 2001). This relatively small cost has led Riisgard *et al.* (1993) to suggest that passive flow is of little energetic consequence to active suspension feeding invertebrates. This view seems to overlook the tremendous potential passive flow has to increase water movement through the filtering structures of active suspension feeders (Vogel, 1974, 1977; LaBarbera, 1977; Young and Braithwaite, 1980; Allanson *et al.*, 1992; the current study) and the subsequent gains in food capture demonstrated for animals utilizing passive flow (Young and Braithwaite, 1980; the current study). Thus, the substantial increases in feeding rates due to passive flow are likely to strongly influence the energetical gains of these organisms, regardless of the magnitude of the effects on feeding costs.

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